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INTER-RELATIONS BETWEEN DEVELOPMENTAL MODELS IN GEOMORPHOLOGY, PLANT ECOLOGY, AND ANIMAL ECOLOGY

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I. SYSTEM AND ENVIRONMENT

The first step in formulating a theoretical model to describe a natural process is to delimit the scope of the model by making a formal distinction between the system, which is the primary object of study, and its environment—those parts of the external world which interact with it (1). Except for the special cases of systems which are completely isolated from the external world, as in classical thermodynamics (or which include it in its entirety, as in cosmology), every natural system is affected in some way by the states of its environment. The validity of a model of a system, and of the description of the system which it provides, will then depend not only on the characters of the model but on the assumptions made about the environment and its interaction with the system. In general, it is reasonable to assume that the behavior of the model will not be sensitive to small changes in the behavior assumed for the environment. In particular, the system is likely to be more or less independent of assumptions made about processes in the environment which take place on a sufficiently small scale (e.g., in time or in space). However, the assumption of large-scale order in the behavior of the environment is likely to result in the imposition of large-scale order on the behavior of the model. Such an effect may be mistaken for a deduction within the model if the assumptions made about the environment are not formulated explicitly.

System and environment in animal ecology

Theoretical models in animal ecology fall into two general types: those in which the system under study is an entire animal community and those in which it is restricted to one or a few species. In both cases the environment of the system includes the vegetation, climate, and (more remotely) the geology and landscape; in the second type of system it also includes the remainder of the animal community. The validity of the models then depends on the assumptions made, explicitly or implicitly, about the large-scale properties of the vegetation, climate, landscape, and animal communities.

This paper was occasioned by the observation that most contemporary animal ecologists, when discussing the interrelations of their system (animals) with their environment (habitats), use terms and concepts which characterize the developmental theories of geomorphology and ecology—specifically, those theories related to Davis's cyclic system of landscape development and Clement's "dynamic" system of vegetation. Moreover these terms and concepts—such as "succession," "climax," "equilibrium," "maturity," "stability," "optimization," "resource efficiency"—are being increasingly applied to animal communities themselves, implying the adoption of a developmental theory of animal ecology. Although the developmental theories have an attractive simplicity and a schematic completeness (which appears to be responsible for their continued survival in teaching courses and textbooks), they have been rejected by most contemporary specialists in plant ecology and geomorphology. While most ecologists nowadays use the developmental terms in a loose and imprecise way, it remains to be shown that the implicit assumptions which they represent about long-term development of landscape and vegetation do not condition the conclusions which are drawn about the long-term behavior of animal communities.

This paper includes a brief review of the developmental theories of geomorphology and vegetation, and a summary of a case in which the predictions of the theories were critically compared with observation. Although geological processes do not often affect animal communities directly, the examples quoted will show how oversimplified concepts of geomorphology can affect the formulation of models of plant ecology; in an analogous way, concepts of vegetation can affect models of animal ecology. Finally, we will briefly point out some general limitations of the developmental systems and show how their adoption in animal ecology restricts the types of conclusion that can be drawn about animal communities.

The account of the contending theories in geology and botany is necessarily superficial: a number of detailed reviews have been published (2-5). We will not discuss at all the concept of climatic constancy that formed one basis for Clements's vegetational concepts, but it should be pointed out that its abandonment has caused difficulties for the developmental theories of vegetation.

II. CONTENDING THEORETICAL SCHEMES IN GEOLOGY AND BOTANY

A note on terminology

The classical schemes of landscape description (6) and vegetation (7) are commonly called "dynamic" (Clements's own term) because they emphasize progressive change in landscape and vegetation. In what follows, however, we propose to call them "developmental" schemes because they emphasize change towards a stable end-point. We use the term "kinetic" for theoretical schemes which emphasize continuous change and do not require the existence of an end-point.

William M. Davis's Cycles of Erosion

During the nineteenth century, geological controversy had centered on the problem of whether geomorphological forms were the result of present processes or of cataclysmic events in the past. Davis's theory (6) was built on Lyell's Principle of Uniformitarianism, i.e., that present processes are adequate to explain all of the events which we can see. In applying the principle, however, he assumed that present processes are active in only parts of the landscape, and that other parts have been molded by the same processes acting at earlier times. Davis's assumption was that any present landscape reflects the structure of the bedrock outcrops, the geological processes that are in action, and the stage or period of advance of those processes. He built from these assumptions a pedagogical scheme that has come to be known as "Cycles of Erosion".

His ideas on the process of formation of landscape were influenced by studies he made in the Appalachian Mountain region, and much of his theory is immediately applicable to the landscape patterns visible there. Davis saw many mountain tops with apparently accordant summits; that is, the tops of the mountains, whatever the kinds of rocks involved, appeared truncated at the same heights. He saw that some meandering rivers had cut down through rock strata so as to flow through deep, steep-sided valleys in mountainous regions, while others cut through a mountain ridge and followed the structure of the next valley. Unifying these various observations, Davis developed the concept that at some previous time, which he identified with the Cretaceous, the Appalachian region had been reduced to an essentially level plain, a Peneplain, across which rivers had flowed wherever they happened to meander. Then renewed uplift of the land mass at the start of the Cenozoic (a period of mountain building) resulted in down-cutting of rivers, oversteepening of the stream beds, and therefore more rapid erosion. However, the courses of many rivers, now rejuvenated, were determined by the patterns they had followed on the previous surface, the Cretaceous Peneplain; hence the rivers follow "entrenched meanders" superimposed upon the topography below.

Each epoch of geological history, Davis reasoned, was a cycle of erosion beginning with the uplift of a block of topography of continental size. Once uplift was complete at the start of a cycle, erosion attacked this uplifted area and lowered the topography towards a Peneplain closely associated with the base level of erosion. This base is controlled by the level of the mouths of the draining rivers and is the surface which is inclined just enough to allow rivers to transport the produce of erosion.

The Cretaceous Peneplain, identifiable on the flat tops of the Applachian Mountains from Georgia to Newfoundland (the "Schooley Surface"), was the product of down-wasting during a previous, Mesozoic, cycle of erosion. This cycle had started with the mountain-building which created the New England Alps in the Permian Revolution (which ended the Paleozoic and introduced the Mesozoic).

Davis's ideas of Cycles of Erosion were consistent with contemporary theories of classification of geological time. Historical geology was built on the idea that there have been major periods of mountain-building in the Cambrian, in the Permian, and at the end of the Cretaceous, thus at the beginning and end of the Paleozoic and at the beginning and end of the Mesozoic. Within each of the major periods of geological time there were epochs, each of which was defined by a minor period of geological revolution (uplift and mountain-building).

The description of landscape in Davis's terms

At the start of an epoch, following uplift, topography will be, in Davis's allegorical sense, youthful. There will be broad, flat-topped uplands (the remnants of the previous cycle) between the river valleys, and youthful streams, fast-flowing, steep-valleyed, which will have many falls and rapids. The streams erode rapidly at their headwaters. As topography and streams mature, the valley-sides become gentler and then slopes meet at the divides between river systems. The stream, when mature, is graded to its bed throughout its length; that is (i) the grade is steep in the headwaters (streams carry off materials more rapidly than they are produced by erosion), (ii) the grade is at equilibrium in the region of the mature stream (erosion balances what the stream can carry off), and (iii) the grade is low in the lower reaches of the stream (more material is brought to the stream than it can carry away). Stream maturity occurs when the whole system is adjusted. This event is essentially momentary, when all streams in the drainage basin are adjusted to a base level and able to carry off their load. Before the moment of maturity, large areas of slope and surface are still in the erosional context of the previous erosion cycle. After the moment of maturity, many areas are no longer adequately drained and are thus removed from the present cycle of erosion.

In old age, the stream meanders across a broad plain, unable to remove the products of erosion brought down to it, i.e., it approaches the base level of erosion. During old age, large areas of the erosion basin have been abandoned by erosion and are stable surfaces, in essence, peneplain elements. The original uplifted surface has been removed except in remnants preserved because of their resistance (hartlings) or their remoteness (fernlings) from the river. The Peneplain, once established, persists until it is eroded by processes set in motion by further uplift.

Plant Succession

The concept of Succession to a stable, self-perpetuating community is the intellectual analogue in botany of the development of landscape to a stable peneplain.

Cowles (8,9) described differences among plant communities on the Indiana sand dunes, correlated with distance from the Lake Michigan shore. In so doing, he assumed that distance from the lakeshore was correlated with the age of the dunes. This correlation is built on the assumption that spatial differences in vegetation and soil are a mirror of temporal events, not only of stability and shelter.

Cowles described in detail the sequence of vegetation types: (i) the vegetation of the active, blowing sand of the beach, (ii) the vegetation of the dunes where marram grass consolidates the sand, (iii) the vegetation of the sheltered backs of these dunes, and so on. He concluded that through the years the vegetation consolidated the sand; then dead vegetation collected, building up soil; on this soil other plants were able to grow, their remains further leading to the development of better soils, allowing forest trees to grow. He reasoned that with increasing age there was an increasing soil stability, development of the soil profile, and a succession of vegetation.

Frederick E. Clement's developmental scheme of vegetation

Clements grew up in the sand hills of Nebraska and formulated the concept of the prairies as natural vegetation, in contrast to the traditional American view of the grasslands as "the Great American Desert." He developed the idea that the great vegetational regions were not only natural but keyed to the climate of the region. Clements was influenced by Cowles's studies of plant Succession. But his ideas of evolution toward stability were probably also influenced by the general late nineteenth century assumptions of determinism and of social evolution and adjustment toward balance of political power and stability. Davis's stable old landscape surfaces, uniformly and thickly carpeted with matured soils in which local soil and rock differences were eliminated, provided the substrate upon which competition among plant communities would determine which will finally dominate the landscape. The idea that the Schooley Surface had existed since Cretaceous time had great impact upon botanists, who took the concept literally: if the surface existed during the Mesozoic, it must have been available for the persistence and development of vegetation. In Clement's scheme, plant succession is:

> . . .the process through which tightly organized groups of species called associations interact with their substratum to modify their habitat and pave the way for occupation by other associations not previously able to occupy the habitat. According to this generalization, the outcome of successional developments is determined primarily by the climate because the characteristics of the substrate undergo extremely slow and orderly change related to the formation, uplift and dissection of one or more peneplains. [(17), p. 61]

The eventual outcome of this slow and orderly change was supposed to be a fully adjusted, and hence unchanging, vegetational formation, which Clements called Climax. The word Climax was related to regional climate. Its association with the idea of a culmination of a sequence of developmental processes came later and was secondary, but the analogy between Peneplain and Climax is clear.

The successional sequence, which Clements called the sere, is the second major element in his theoretical scheme. Following disturbance, in the process known as recycling, the vegetation retraces and displays the stages of development and establishment of the normal "mature" formation. The major stream of development Clements called the prisere; the establishment, competition and replacement of species in plant communities he called ecesis. He considered the effects of disturbance by fire, erosion, and factors such as local soils, temporary; hence the changes resulting from these were called secondary succession, but they also return the vegetation to the normal equilibrium—the Climax.

Clements saw in Succession the maturing of the vegetation, a process similar to the stages of a life cycle of an individual:

> The unit of vegetation, the climax formation, is an organic entity. As an organism, the formation arises, grows, matures and dies. Its response to the habitat is shown in processes or functions and in structures that are the record as well as the result of these functions. Furthermore, each climax formation is able to reproduce itself, repeating with essential fidelity the stages of its development. The lift history of a formation is a complex but definite process, comparable in its chief features with the life-history of an individual plant. The climax formation is the adult organism, of which all initial and medial stages are but stages of development. . .a formation, in short, is the final stage of vegetational development in a climatic unit. It is the climax community of a succession that terminates in the highest life-form possible in the climate concerned. [(7), restated in (10), p. 161]

He visualized each vegetation stage preparing the soil for the next vegetation to occupy the site. He hypothesized a system of development whereby communities replace each other in succession until the stable equilibrium vegetation occupied the site. Each formation had its characteristic stages of succession or maturation.

Some botanists, and many zoologists, nowadays use the term Succession in a weaker sense, to refer merely to the sequence of changes which follows disturbance of vegetation. Clements, however, as is clear from the above quotation, used the word to imply progressive replacement of communities, preparation by each stage for the vegetation of the next stage, and progression towards a predictable end-point that is determined by the climate and not by the intermediate stages. Thus the concept of Succession is intimately connected with the concept of Climax, and each is unintelligible without the assumption of the other.

Clements considered plant species as uniform, consistent with the type concept generally held by botanists at that time. If species, according to the type concept, are uniform, the members of the community will have a fixed and consistent relationship with each other. Reasoning from space to time, as he did in considering Succession, he concluded that because the forest or prairie Climax is consistent over a regional extent, it must also be continuous through time; hence the mutual adjustments among organisms in the Climax result from their association together and the selection pressures which make them fit into the organization. This concept is expressed in the idea that the members of a community react among themselves while the community as a whole reacts with the physical environment (11).

Developmental systems of soil classification

The analogy between the developmental theories of landscape and vegetation is obvious, and the dependence of the Climax concept on that of Peneplain has been demonstrated in the extracts quoted above The direct connection between the two schemes is in the soils, which develop under the influence of both landscape and vegetational processes.

In Davis's scheme, as the erosion cycle starts, bedrock outcrops, falls, and rapids are common, and deep soils persist only on the remnants of the older, higher surface. As the cycle proceeds, soils thicken and develop, especially downstream, so that at the end of the cycle the whole lowland Peneplain is covered with deep erosional and residual deposits. The classical scheme of soil development assumes that mature soil types are associated with mature vegetation types, both being products of a long period of growth and integration under constant environmental conditions.

The mature soils, the Climax vegetation, occur on the deep alluvial or residual deposits of the mature land surface—the Peneplain. Because the Peneplain soils are deep and deposits of the river-borne debris include minerals carried from all parts of the previous drainage basin, they were assumed to be homogeneous, independent of the local rock and spread as a deep blanket over all the surface. Each Climax and soil type is determined by the regional climate which determines the final stable community. Local effects of drainage, topography, and bedrock can only be temporary in the development of mature or climax soils as they are in the development of the Peneplain.

The kinetic schemes of Gilbert and Gleason

Even before the presentation of Davis's theory, an alternative theoretical scheme for the description of landscape development had been formulated by Gilbert (12). His report on erosional processes in the Henry Mountains of southern Utah used a theoretical scheme in which a steady state exists at all times because import of energy and materials is automatically balanced by export. Each disturbance alters the system so that it reaches a new steady state determined by the changed transport of mass and energy. The theoretical framework used is essentially that of the open system (13), (14); open system treatment is especially applicable to a drainage basin, because the form of the basin is determined by the rates of inflow and outflow of materials.

Gilbert's description of stream action depended upon the operation of reciprocal effects upwards and downwards within the system:

> Of the main conditions which determine the rate of erosion, namely the quantity of running water, vegetation, texture of the rock, and declivity, only the last is reciprocally determined by rate of erosion. Declivity originates in upheaval or in the displacement of the earth's crust by which mountains and continents are formed: but it receives its distribution in detail in accordance with the laws of erosion. Wherever by reason of change in any of the conditions, erosive agents come to have locally exceptional power, that power is steadily diminished by the reaction of the rate of erosion upon declivity. Every slope is a member of a series receiving the water and waste of the slope above it, and discharging its own water and waste upon the slope below. If one member of the series is eroded with exceptional rapidity, two things immediately result: first, the member above has its own level of discharge lowered and its rate of erosion is thereby increased; and second, the member below being clogged by an exceptional load of detritus has its rate of erosion diminished. The acceleration above and the retardation below diminish the declivity of the member in which the disturbance originated, and as the declivity is reduced the rate of erosion is likewise reduced.
>
> But the effect does not stop here. The disturbance that has been transferred from one member of the series to the two which adjoin it is then transmitted to others and does not cease until it has reached the confines of the drainage basin. For in each basin all lines of drainage unite in a main line and a disturbance upon any line is communicated through it to the main line and thence to every tributary. And as a member of the system may influence all others, so each member is influenced by each other. There is an interdependence throughout the system. [(12), pp. 117-18]

Reciprocal effects of stream action extend upwards to the point at the very tip of the final division of the drainage which Gilbert considered to be the most sensitive spot of all. Above that, drainage on the slopes is either in sheets or in rills and as a result the shape of the surface changes from concave upward (which is the pattern of a stream) to convex upward (which is the pattern of a divide). The divide is controlled by creep; the stream is controlled by erosion. The reason that the divide is convex is that its motion is most rapid where already steepest. As Gilbert sees erosion, displacement by stream action at the highest tip of drainage has a maximal effect because it changes the focus of the amphitheater, or funnel, of creep and translates its influence throughout that funnel, essentially 180° around the head of the drainage. Because of the oversteepening involved in creep, instability is greatest at headwaters or where streams pass out of hard rocks onto soft rocks.

Hack (3) asserted that a moving equilibrium is established almost as soon as erosion starts and that it exists at all stages with no time variation in the forms as they are developed. Leopold, et al. have shown that both longitudinal and lateral adjustments of the stream bed are continuous (15). Immediate adjustment of channel shape and cross-section occurs at every flood or low water flow, so that the river is always and everywhere adjusted to the instantaneous stream volume, whatever may be its longitudinal profile. Furthermore, Leopold and Maddock (16) have shown that the sediment load is also included in the moving equilibrium, in opposition to Davis's statement that a "senile" river cannot carry the sediment brought down by its head-waters.

Gilbert considered vegetation to be highly important in the process of weathering by discouraging erosion, because by its presence it interrupts the flow of rain and by its roots it holds the soil. Thus in the Henry Mountains, the slopes on the higher peaks where there was more rainfall were vegetated and rounded, whereas the ridges on the lower hills, where there was less rainfall and little vegetation, were abrupt and sharp. (In the scheme of Cycles of Erosion, the upper rounded slopes would be identified as uplifted, partially dissected remnants of a previous erosion cycle.)

According to Gilbert (17), down-wasting of the land surface occurs on all surfaces essentially at the same time; the whole land surface, its valleys and its uplands, are all being eroded simultaneously and constantly, instead of having some elements actively attacked and reduced while other parts of the topography are abandoned. Furthermore, the idea that episodes of mountain building have been intermittent or cyclic has latterly been replaced by a concept of very slow and continuous uplift (3). Thus changes in landscape form should not simply reflect processes of running down, but adjustment between rates of uplift and rates of down-cutting.

Gleason's individualistic concept of the plant association

At the same time that Clements constructed his developmental model of vegetation, Gleason in the United States, Fournier and Lenoble in France, and Ramensky in Russia formulated kinetic models. Gleason (18) recognized the usefulness of plant associations:

> Plant associations exist; we can walk over them, we can measure their extent, we can describe their structure in terms of their component species, we can correlate them with their environment, we can frequently discover their past history and make inferences about their future. . . .
>
> We all readily grant that there are areas of vegetation, having a measurable extent, in each of which there is a high degree of structural uniformity throughout, so that any two small portions of them look reasonably alike. [(18), pp. 8, 9]

However, he went on to point out the continuous gradations in the species constituents of associations:

a) Associations are vaguely defined. Where the change in the environment is abrupt, the transition line in vegetation is sharply defined and narrow. Where there is a gradual transition in the environment, there is a correspondingly broad transition zone in the vegetation.

b) Associations have arbitrary geographic boundaries and no two areas of similar vegetation are identical in species composition. Plants typical of one community are often found in many other types of vegetation; it cannot be told whether these isolates are fragments or embryos of a vegetation association.

Lake shores in the same region, for example, have similar vegetations, yet the glacial lakes from Maine to Saskatchewan differ gradually so that

> . . .westernmost and easternmost of the series, while still containing some species in common, are so different floristically that they would scarcely be regarded as members of the same association.
>
> No ecologist would refer the alluvial forests of the upper and lower Mississippi to the same associations, yet there is no place along their whole range where one can logically mark the boundary between them. [(18), p. 14]

c) Vegetation structure in one spot varies from decade to decade so that associations originate and disappear with varying speed.

> And just as it is often difficult and sometimes impossible to locate satisfactorily the boundaries of an association in space, so it is frequently impossible to distinguish accurately the beginning and end of an association in time. [(18), p. 13]

d) The same environment may have different vegetations, e.g., the deserts of Australia and Arizona, and the treeless highlands of Chiliean Andes or Oregon Cascades. The same vegetation may occur in different environments, e.g., White Pine forests in Massachusetts and Michigan, prairie grasslands in Illinois and Nebraska, cedar swamps in Indiana and Florida.

The vegetation of an area, Gleason concluded, is the result of two factors: the fluctuating and fortuitous immigration of plants and an equally fluctuating and variable environment. As a result of constant seed immigration, every plant association is regularly sown with seeds of numerous extra-limital species, as well as with seeds of its own normal population:

> . . .every plant association tends to contain every species of the vicinity which can grow in the available environment. . . . Each. . .is fully entitled to be recognized as an association and there is no more reason for regarding one as more typical than another. [(18), pp. 18-19]

The last sounds analogous to the appearance of the population concept in modern systematics, as does:

> This diversity in space is commonly overlooked by ecologists, most of whom of necessity limit their work to a comparatively small area. . . . [(18), p. 15]
>
> Under the individualistic concept, the fundamental idea is neither extent, unit character, permanence, nor definiteness of structure.
>
> It is rather the visible expression, through the juxtaposition of individuals, of the same or different species and either with or without mutual influence, of the result of causes in continuous operation. [(18), p. 25]
>
> . . .
>
> In conclusion, it may be said that every species of plant is a law unto itself, the distribution of which in space depends upon its individual peculiarities of migration and environmental requirements. Its disseminules migrate everywhere, and grow wherever they find favorable conditions. The species disappears from areas where the environment is no longer endurable. It grows in company with any other species of similar environmental requirements, irrespective of their normal associational affiliations. The behavior of the plant offers in itself no reason at all for the segregation of definite communities. Plant associations, the most conspicuous illustration of the space relation of plants, depend solely on the coincidence of environmental selection and migration over an area of recognizable extent and usually for a time of considerable duration. A rigid definition of the scope or extent of the association is impossible, and a logical classification of associations into larger groups, or into successional series, has not yet been achieved. [(18), p. 26]

The kinetic scheme in soil classification

The connection between landscape processes and vegetation is directly mediated by soils in a kinetic scheme, too. Soils develop under the influence of weather, landscape processes, and vegetational activities and products.

Nikiforoff has shown that development of a mature soil profile is rapid and closely responsive to the vegetation on the site (19), (20). Olson's (21) reanalysis of soil processes on the Indiana dune site of Cowles's classical work emphasizes the same point. Soil profile development in Nikiforoff's scheme is the expression of a steady state of outflow of materials so that organic matter, dissolved minerals, and clay-sized particles are removed as fast as they are added. Within this context we can visualize all hilltops, slopes, and valley bottoms lowered by creep, corrasion, or buried by sediment in a continuum while soil processes, determined by the local vegetation, maintain mature soil profiles in a steady state during down-wasting.

III. A CASE HISTORY

The Appalachian mountains and forests revisited

Braun made a comprehensive analysis of the regional vegetation of eastern North America on a developmental basis (22), (23). Her study (22) of the forests of the Appalachian Mountains, together with Davis's work on the geology of the same region (6), represents the definitive attempt to describe this region in terms of the developmental models of Davis and Clements.

Subsequently Hack, a geomorphologist, and Goodlett, a botanist, have worked together in the center of this classic region, the Shenandoah Valley of northern Virginia. In a comprehensive paper (17), they have compared interpretations of their observations provided by both "developmental" and "kinetic" models. They contrasted the assumptions of the two schemes and their relative merits in clarifying the observations.

The developmental interpretation

According to Davis, the flat tops of the mountains show accordance of summits and discordance of structure. They are remnants of an uplifted, partially dissected Cretaceous Peneplain—the "Schooley Surface." Another partially developed Peneplain is shown by the high shoulders of many valleys, the "Harrisburg Partial Peneplain," the product of a later and incomplete cycle of erosion. These surfaces have been identified in Hack and Goodlett's study area (24). On these surfaces one would expect development of deep, mature soils and the mature Climax forest. Expressing this, Braun took the long view of geomorphological and vegetational process:

> Here also, physiographic history seems to have had a profound effect upon the nature of present-day vegetation. On the ravine slopes formed in the latest erosion cycle, the vegetation is developing in response to present forces, both topographic and climatic. Although very limited in extent, it seems logical to assume that mixed mesophytic forest is the potential climax of the area; that by its development the extent of the mixed forest, greatly restricted at one or more times in the Tertiary and early Pleistocene, may expand east-

> ward into what we now know as the Oak-Chestnut region. The outliers are forerunners in a development which would take thousands of years to complete, for it must await development of land surfaces and of soils no longer related to the Harrisburg cycle. That these mixed mesophytic communities are not relics of a former more extensive mixed mesophytic region (mixed forest of the Tertiary) seems certain because of their limitations to surfaces produced in the last (or present) erosion cycle. [(23), p. 242]

The kinetic interpretation of landforms

Hack (17) found that the measured profiles of ridge crests and the convex upper slopes of mountains could be described by simple power functions of the form

$$H = CL^f,$$

where H is the fall from the ridge crest, L is the horizontal distance from the ridge center, and C and f are constants, which define the steepness and curvature of the slope respectively. Although C and f vary over a wide range from ridge to ridge, they were found to obey closely an empirical relationship which was the same for different substrates. Thus the shapes of the upper parts of the mountains follow a universal empirical law and therefore can be understood as resulting from contemporary erosional processes. The assumption that the upper mountains are the remains of an ancient Peneplain is not only unnecessary; it requires that the empirical law be dismissed as a set of coincidences.

Furthermore, other geologists have pointed out the close relation between the altitude of the mountain ridges of the region and the structure and physical properties of the bedrock (25), (26). Hack and Goodlett (17) showed that all the higher mountains in their study area correspond to the Pocono sandstone, the most resistant rock of the area.

Hack (27) has subsequently shown that the gradients of the "Harrisburg Partial Peneplain" can also be related to present-day drainage, without invocation of hypotheses of uplift and partial dissection in the past.

The kinetic interpretation of vegetation

Summarizing studies of the distribution and interrelations of the tree species, Goodlett (17) reported that the present distribution of many of the tree species as well as the forest types is closely related to topography, orientation of slopes, and the nature and altitude of the bedrock. The main unifying principle underlying the coincidences is water. Thus on the hot, dry ridges and noses he found a forest type characterized by yellow pines (Pinus rigida and P. pungens), in the hollows where the microclimate is cooler and moister he found forests characterized by northern hardwoods (Sugar Maple, Acer saccharum; Basswood, Tilia americana; Yellow Birch, Betula lutea), and on the intervening slopes he found varied oak forests containing none of these species. Sugar Maple and Basswood, together with Tuliptree, Liriodendron tulipifera, are listed as the three dominant species in the "mixed mesophytic forest" which Braun (23) regarded as the potential Climax of the region.

> Concave areas on slopes, which characteristically support northern hardwood forest, are the product of the geomorphic process of stream sculpture. However, once formed by stream sculpture, a concavity undergoes erosion and grading largely by creep, which is encouraged by the same moist conditions that seem to determine the distribution of the northern hardwood forest type. Convex areas on slopes characteristically support yellow pine forests; therefore, the distribution of yellow pine forests is related to the distribution of land-forms created largely by the process of creep. Rates of creep probably are extremely slow on these noses and ridge crests because the environment is dry and because the volume of material originating on the slope above is less. Dryness presumably controls the presence of yellow pine forest. Convex areas thus tend to be more stable habitats for plant growth than concave areas, and the yellow pine forest probably undergoes less disturbance than the northern hardwood forest. It can perhaps be said, then, that the yellow pine forest is characteristic of relatively stable areas whereas the northern hardwood forest is characteristic of relatively unstable areas. [(17), p. 59]

This, of course, is a contradiction of the idea of Succession through pine stages towards a stable Climax of a complex northern hardwood forest type.

Furthermore, the greater diversity of the hardwood forests on the flood plains appears to be maintained not only in spite of their instability, but because of their instability. Studying an area devastated by a flood six years earlier, Goodlett [(17), pp. 49-51] found that the bare areas created by the flood had been reseeded by nearly all the tree species that generally constitute the bulk of both the forests of the flood plain and slopes, and lacked only a few of the species found in the hillslope (older) forest. He suggested that "in large part, the greater number of species in the damaged flood-plain may be the result of periodic inundation by seed-carrying flood-water". Working in a nearby part of the Appalachian Mountains, Whittaker (28), (29) has similarly been unable to confirm by empirical evidence the implications of the developmental sequence; he found no consistent relations between diversity, community productivity, disturbance, and succession. The northern hardwood forests in moist cove valleys are characterized by high rates of primary production, but even higher rates were found in disturbed areas (28). According to the developmental theories, biomass, production, diversity, uniformity, efficiency, and stability should all increase with Succession and reach maxima in the Climax [for review see (4)].

Vegetation and soil erosion

Hack and Goodlett (17) began their study to investigate the results of a spectacular local flood which had devastated some of the valleys six years earlier. In the developmental systems, vegetation and stable mature soils combine to offer each other maximum protection. In the study area Braun (23) had identified the theoretical "mixed mesophytic forest" as the potential Climax and considered all other types of forest as transitional or successional. Most of the area had been logged in the late nineteenth century, so it is thus logical within this system to consider the resulting second-growth forest as "inferior" or "immature." Accordingly, the U. S. Forest Service reported on the flood:

> Most of the landslides started on steep slopes near the tops of hog-backs or divides. In these areas, natural regeneration has been slow. It consisted of inferior young stands of rather open and brushy type. In general, slides did not occur where thrifty, normal stands had developed. In fact, when some slides reached better stands, the slide was restricted in width and a few slides stopped altogether.
>
> This storm showed how long it takes land to recover fully from past abuse. It showed the urgency for early initiation of good land use and management practices. . . . [(30), pp. 31-32]

To attribute the flood damage in this way to the "inferiority" of the vegetation carries the implication that stable mature vegetation would have prevented it. Arguing against this, however, Hack and Goodlett pointed to debris from older landslides which had occurred prior to the disturbance of the forest by logging, and showed that the assumption that undisturbed forest protects the soil from landslides leads to a contradiction.

> Compound debris fans are unequivocal evidence of food damage to slopes in the past, prior to the period of logging, and probably prior to the time of settlement by the white man. Either the forests mantling the slopes in the past were not all "thrifty normal stands"—a possibility—or the slope forests, regardless of quality, cannot control huge volumes of runoff. There is a limit to the amount of runoff that a forest can withstand. This limit determines the density of drainage channels, and were there no limit to the protective powers of the forest there would be no stream channels at all. [(17), p. 56]

If the maturation of vegetation were a consistent process, one would expect that, by the effects of Succession, progressively older landslides would contain tree species progressively more similar to the regional norm, but Goodlett found the species composition on the oldest landslides to be indistinguishable from that of the young growth on the newest slides.

Summary of the kinetic interpretation

Summarizing their results, Hack and Goodlett state:

> The present distribution of many of the tree species as well as of the forest types is closely related to topography, orientation of slopes, and the nature and attitude of the bedrock. . . . [(17), p. 32]
>
> . . .
>
> The most important lesson to be learned from the landforms of the Little River area relates to the extraordinary regularity of the landforms and the nicety of adjustment of the soils and vegetation to them. The close relation between these three terrain elements has been demonstrated over and over again in the preceding pages. The correlation extends even to the asymmetry in their distribution pattern. The explanation for the relation is that the mountains are shaped or graded in such a way that the products of decay of the bedrock can be moved across the ground surface and carried off in the channelways out of the area. Various processes that differ in relative effectiveness in different parts of the valley act to transport the debris, so that the graded slope must also be different from one part of the valley to another. The resulting regular forms are the product of this adjustment in a region where the underlying bedrock is rather uniform. As time goes on, the entire landscape is lowered. Though the slopes may flatten through time, the entire mountain mass retains a form graded for the transportation of waste materials.
>
> The vegetation reflects the local differences in process, slope, and environment. Difference in forest type within one valley are often as great as the regional differences between the forests of the northern Appalachians and those of the southern Appalachians. The magnitude of these differences is a reflection of the extreme diversity in the physical environment between different parts of the valley. [(17), pp. 57-58]

As they pointed out (p. 58), the picture envisaged is that of a steady state in an open system (2). The steady state is shifted by short-term disturbances, such as flash-floods, by medium-term disturbances, such as changes in climate or in the frequency of floods, and by long-term disturbances, such as the steady reduction in relief produced by continuous erosion. In each case those parts of the system whose time-scale is shorter than that of the disturbance react to produce a new steady state. This type of moving equilibrium is characteristic of open systems (13).

Failures of the developmental interpretation

Of the six major predictions of the developmental theories, all are inconsistent with Hack and Goodlett's observations. The summits are not "discordant in structure": all can be related to the same strata of resistant rock. The form of the upper slopes conforms to a universal law which reflects active erosion and is thus inconsistent with the concept of an older Peneplain, as yet uneroded in the present cycle. The Climax is found on the most unstable areas, not on the theoretical Peneplains. The diversity of the forest type which approximates most closely to the theoretical Climax appears to result from repeated disturbance, not from long development. Mature forests failed to protect mature soils from erosion, even in the epoch before man's interference. There is no evidence of vegetation development on progressively older landslides.

None of these discrepancies necessarily undermines the structure of the developmental theories; each could be attributed to a defect in interpretation within the structure. Thus, for example, it could be argued that the Cretaceous Peneplain lay above the Schooley Surface and has already been fully eroded. Or it could be argued that the theoretical Climax forest has not yet evolved; in other words, that the entire vegetation of the region is Successional. Yet to argue thus, that Peneplain and Climax no longer exist, or do not yet exist, even in the classic area for their identification, would seem to change the concepts almost into the nature of myths. In fact, it is easier to explain the conflict between theory and observation in terms of the structure of the model.

In a kinetic theory, observed forms are analyzed in relation to observable processes; only when discrepancies appear does it become necessary to invoke hypotheses about past events. In the developmental theories, however, the assumption of stable equilibrium is made at the outset: when only change is observed, the assumed equilibria must be placed in the distant future and distant past. It then becomes less important to describe the processes of development than to identify the stage of development and the elements which will become important in the distant equilibria. When attempts are made within the developmental theories to identify frozen or partial equilibrium states in the present landscape, the predictions are often found to be incorrect; but this can be attributed merely to errors in identification. The defect of the developmental theories is, then, not that they fail to make correct predictions, but that they are based on assumptions which are unnecessary and unverifiable.

IV. DEVELOPMENTAL THEORIES IN ANIMAL ECOLOGY

Another review of these controversies, already debated for decades, may seem unnecessary and irrelevant to modern issues. The developmental theories of geology have almost disappeared from modern writings; and although recent textbooks of plant ecology continue to use Clements's terminology, in nearly all it is heavily qualified and the deterministic aspects of his theoretical scheme are little stressed. But the developmental scheme, with its attribution of organismic characteristics to communities, appears in some of the most recent textbooks of general ecology, especially those intended for introductory teaching courses.

> In terms of the expressions (1) of the preceding chapter, succession is the result of an indefinite iterative process with a stationary end state to which the variables tend. A set of conditions controls a set of rates of change of the same conditions, and the whole state is directed toward an asymptotic steady state. This could properly be called a climax. [(31), p. 33]
>
> . . .
>
> By and large, succession seems to be a characteristic of the community itself; it results from the fact that the action of the community on the habitat tends to make the area less favorable for itself and more favorable for other sets of organisms—that is, until the equilibrium or climax state is reached. [(32), p. 259]

A pair of modern high school textbooks written and published under the auspices of the American Institute of Biological Sciences presents as extreme a concept of Succession as any since Clements.

> If we believe that a forest, like an organism, is born, grows and changes, then we must have evidence to support this hypothesis. . . .For example, biologists can study fields that have been abandoned by farmers and allowed to return to the natural state. . . .
>
> The changes that occurred in these abandoned fields and that eventually led to the establishment of the oak-hickory forest occurred in a sequence. . . . The process of change and enrichment ended in this case with the formation of the oak-hickory forest. . . .
>
> Through succession the community developed from a few pioneer species, which were able to utilize only a small part of the environment resources, to a mature community which persists for long periods of time by making full use of the environmental resources. . . .
>
> The new organisms slowly replace the pioneers; then they dominate the community until their activities alter the environment. Eventually, they are replaced by better-adapted forms. One important effect of this process of replacement is to produce, at each succeeding step, a community that tempers the environment more successfully than its predecessors. . . .
>
> As the number of species in the community increases, the niches available for energy utilization are increased and filled. As the community becomes more complex, the cooperative and competitive relationships among the populations increase. These, together with the alteration of the environment, can have but one effect. Those populations best adapted to the new conditions survive and replace the less fit. The end result is a mature community. . . .
>
> Eventually the species of the area form a stable community, which is called the climax community. . . . [(33), pp. 655-658]
>
> . . . .
>
> A forest of this kind represents a reasonably stable environment—a climax community. Unless some new event alters conditions drastically, the succession of plants and accompanying animals has essentially ended. The wound in nature has been healed. [(34), pp. 173-174]

Apparently the developmental concepts are regarded as useful unifying principles in general ecology (35), (31), whatever their defects in application to real plant communities. At the same time the scheme of succession through seral stages to a stable, efficient, productive Climax community, although rarely expressed in Clementsian terminology, is appearing increasingly often as a basic assumption in theories of animal ecology. It therefore seemed desirable to review yet again the restrictions imposed by this scheme on botanical thinking, and to project these restrictions into animal ecology to suggest some of their likely effects.

Developmental models in animal ecology

There are two broad types of model in animal ecology which utilize the assumptions of the developmental theories.

The first comprises those models in which the animal community is the system and the developmental assumptions are applied (explicitly or implicitly) to the plant community which constitutes the environment. In these theories the vegetation is treated as the habitat background within which the animals interact; the effect of the developmental assumptions is that they prescribe a predetermined sequence of changes and an ultimate stable equilibrium in the environment. This has three important consequences:

1. It results in a substantial decoupling of the system from the environment. Just as the adoption of a deterministic model for the evolution of landforms provided an independently specified description of the environment within which the vegetational system develops, so the inclusion of the vegetation in the same deterministic model provides an independently specified description of the environment of the animals. When a correlation is observed between the structure of the vegetation and the complexity of the animal communtiy (36), this must then be interpreted as cause and effect respectively (37): the reciprocal effect of the animals on the structure of the vegetation must necessarily be excluded from the model, because the structure of the vegetation is ex hypothese determined by Succession—"a characteristic of the community itself." Clements's insistence (10) that the Climax vegetation is determined only by the regional climate is the prototype for this decoupling: the distribution of grassland, for example, determines the distribution of the grazing herbivores, but the latter are not considered to affect the distribution of the grassland by eliminating invading plants from other formations. In a rigid extension of the theory to animal ecology, the animals will themselves form a Climax community determined by the regional climate, and no interactions between animals and plants need be considered at all.

2. The assumption that plant associations follow one another in an orderly succession, until a perennial and spatially consistent Climax is reached, leads to the typological concept of habitats as discrete and classifiable units. The task of descriptive animal ecology then becomes the association of animal communities with these habitat units (38), (39), and that of quantitative animal ecology becomes the interpretation of interspecific interactions within the units (37), (40), (41). Evidence which is interpreted to mean that animal communities rapidly reach equilibrium with their habitats (41), (42) then predicts that animal communities should form discrete typological units matching the habitats. Within such a scheme the succession of animal communities is regarded as a consequence of plant succession (43), and the interrelations of animals in the Climax communities (where they exist) must be a consequence of interactions (e.g., competition) in the past. In particular, the mature animal communities must be matched with the mature plant communities, ex hypothese perennial, and must migrate with them as climatic conditions change. The habitat requirements of individual species, at least in the Climaxes, must thus be attributed to events in the distant past (44). The limitation of such models is that they preclude enquiry into the reasons for regional differences, or historical changes, in the habitat preference of single species: non-conforming species must be dismissed as anomalous or successional and hence outside the scope of the model. When it is found that the distribution of a group of animals as a whole is not well correlated with that of the habitat units, as was pointed out for birds by Peterson (45) as early as 1942, it can then be argued that the whole system has not yet had time to mature. The assumptions of the model are thus in a sense unfalsifiable, because it leads to specific predictions only for Climax communities, which are identified only by agreement with the predictions, and are projected into the future where agreement cannot be found.

3. Another consequence of the typological view of habitats is the distinction between "within-habitat" and "between-habitat" structural properties of animal communities (37). To be self-consistent, such a distinction must remain the same when a larger area is sampled, and this is only possible if the habitats are spatially consistent. However, if an inconsistency is observed, this can be attributed to erroneous identification of the "habitats" (36), (37). In practice, there is an almost unlimited number of ways to divide the vegetation of an area into habitats, so it is impossible to falsify deductions from a model that assumes that the diversity of an animal community depends in some functional way on the vegetational units which comprise its environment.

The second type of model in animal ecology is that which applies the developmental scheme explicitly to the animal community. As shown above under 2, these models arise logically from the use of the developmental scheme to describe the vegetation, just as Clements's system arose naturally within the developmental scheme of geomorphology. Likewise, all these models require a developmental classification of the vegetation, and many of them include it explicitly.

One limitation of these models has already been pointed out above—the practical difficuty of identifying Climax formations as consistent associations of animal species in space or time. Partly to circumvent this difficulty, other models identify stages in animal Succession by means of other properties which theoretically change in a deterministic fashion. As Margalef (31) points out, different authors disagree on the most significant properties to use, but the four most common are diversity, stability, efficiency, and productivity. The limitation of all these models is that special mechanisms have to be devised to accommodate these theoretical properties within the framework of natural selection. Thus the assumption that stable communities are more permanent than unstable ones requires that natural selection should act to prevent protracted increases or decreases in a species' population (46). Such an action is contrary to orthodox concepts of natural selection (47), but these can be circumvented if we invoke some form of group selection [(48); (42), p. 152]. Such mechanisms are necessary under the assumptions of the developmental models, and the assumptions themselves are not in practice falsifiable. If, for example, we go into the field and find that diversity and production reach higher values in early successional stages than in late successional stages (28), it can always be argued that the successional sequence has been wrongly identified, or that the Climax has not yet had time to evolve to maturity. Again we find the characteristic property of the developmental models, that they make predictions about the behavior of elements of the system which can only be identified by reference to the predictions, and need not be present at all in the present epoch.

CONCLUSION

In this paper we have been concerned to make two main points. First, the behavior of the models one makes of systems are conditioned by assumptions made about the long-term behavior of their environments. To assume that landscape develops in a preordained course to a stable equilibrium predetermines that vegetation, and hence animal communities, will also do so; moreover, the structure of the model itself excludes reciprocal action of animals on the development of vegetation, and of plants on the development of landforms. Second, the assumptions of the developmental models limit the type of question which can be asked within the framework of the model. This is not to say that the assumptions and the conclusions drawn from them are necessarily wrong, but rather that they preclude their own falsification. The main advantage of the kinetic type of model is, then, that it includes the developmental model as a special case. In general, ecological systems comprise a large number of sub-systems, each proceeding on a different time-scale. The main restrictive feature of the developmental models is that some of these time-scales (e.g., those for reciprocal actions, for orogenesis, for immigration and evolution of new species, for local extinctions and reseeding) are made indefinitely long compared to other time-scales of interest: the effect is to place significant events far into the future or into the past. In the kinetic models, these time-scales remain finite: if any are really very long, this can then be established by deduction and observation. Thus stable, efficient animal communities may in fact exist now, in the future, or in the past, but this cannot be established by assuming that they must have done so in an ancient Climax, on an ancient Peneplain.

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